THE ANATOMY OF THE LARVA OF CECIDOMYIA RESINICOLOIDES WILLIAMS.

By Francis X. Williams.

In the January number of Entomological News, Vol. XX, 1–8, 1909, I described this midge in its egg, mature larval, pupal and imaginal instars, and gave a brief biological report on it. The curious habit of the larva in living in a mass of exuding resin might be expected to have brought about some adaptive modifications of its structure, especially perhaps of its tracheal system. It is for this reason particularly that the attempt has been made to study the larval structure in detail. As much of the anatomy of the larva is described here as could be worked out in a limited time, and although over a hundred larvae were examined and dissected, the results are far from complete. Considerable difficulty was encountered in tracing out the various systems of the larva, and the writer has deemed it best to omit the doubtful things and to declare only those facts which were made manifest over and over again by the examination of a large number of specimens.

The work embodied in this paper was done in the entomological laboratory of Stanford University.

EXTERNAL ANATOMY OF THE LARVA.

Head, Pl. I, Figs. 1 and 2. The head is very small and imperfectly developed. Its brownish-black chitinized portion consists of a broad irregular ring from which a pair of prong-like rods project well into the supernumerary segment. These rods diverge posteriorly, are more heavily chitinized than the ring, and have muscles attached to them that run from the body wall. The antennae are short, conical, obscurely two-jointed processes placed well above the opening of the mouth. Ratzeburg and L. Defour believe these processes are palpi, but Osten Sacken as well as Laboulbene and Perris, from the position of these organs, consider them rudimentary antennae. I incline to the latter view since they are situated latero-dorsally on the anterior part of the ring and well above the mouth opening. This latter consists of a soft, fleshy swelling taken by Ratzeburg for the labium.

Breastbone, Pl. I, Fig. 3. Ventrally on the posterior half of segment I, and situated in a sort of fold is the "breastbone,"

also known as the "sternal spatula" or "anchor process," an organ said to be peculiar to the *Cecidomyidae*. This is a brownish chitinized process varying somewhat in shape, but usually widest at the extremities, slightly constricted at or near its middle and at the caudal end, and somewhat incised anteriorly where a small portion of it projects beyond a transverse fold. The caudal extremity is concealed under the posterior fold of segment I. The anterior incised portion of the spatula is somewhat scooped out, and the more heavily chitinized central axis sends out a ridge on either side of this depression. Otherwise the whole piece may be quite uniformly chitinized. A lateral view of this organ shows that it follows the curved outline of that part of the segment in which it lies.

The use or the homology of the "breastbone" has been a subject of some speculation. Giard (8) says that some of these Cecidomyid larvae have the power of leaping, using their well developed spatula and terminal corneus papillae for this process, and in this wise: the larva bends itself almost into a circle, and hooking together the breastbone and papillae breaks the connection thus formed and the spring occurs. In the species referred to by Giard however the spatula is well musceled, strongly chitinized, projects well externally, and the corneus papillae are developed. The advantage gained by this faculty of leaping is, according to Giard, the assurance of the dissemination of the species, which in turn insures an abundant food-supply and therefore the successful perpetuation of the species. The larvae of *Diplosis loti* and *jacobeae*, cited as examples by him as having this leaping power, are gregarious and would not leave enough food for their descendants if they were not thus motile. This theory does not seem adequate inasmuch as the adults look after the food-supply for their progeny, and being active and winged, would have no difficulty in finding another suitable plant on which to oviposit. The motile habits of the larva brought into play just before pupation would indicate a search on the part of the insect for a proper place for pupation, the pupa being formed underground and probably at no great distance from the abandoned food-plant. In *C. resinicoloides* the spatula is not well developed, projects but slightly anteriorly, and the posterior corneus papillae are absent, also as the insect lives both in the larval and pupal stages in pitch, the breastbone could hardly be used as a locomotor organ. In fact it does not appear to be con-

nected with any muscles. Owing to the medium in which the larva lives, it is possible that it has lost this power of leaping by the degeneration of the organs so well developed in the saltatorial Cecidomyid larvae. Locomotion in the larva of *C. resinicoloides* is chiefly, if not wholly, accomplished by the extension and contraction of its spiny segments, with the possible assistance of the pseudopod-like processes.

Another theory advanced to explain the use of the breastbone is that it is used as a perforator (17). It could thus be used in some gall-forming species which pupate outside their gall, to force an exit therefrom. L. O. Howard (11) refers to a view proposed by Enock and sustained by Marchal according to which the spatula is used to reverse the position of the larva in the puparium. In the case of *C. resinicoloides* this last theory might apply, but it seems more probable that the spatula is used in making the cocoon, in pushing out a space in the resin, and forming the thin, convex cocoon cap. Inasmuch as, according to Giard, the spatula is only fully developed in the last moult, it is quite evident that this organ is intimately associated with the prepupal actions of the larva. Osten Sacken says (14): "If the supplementary (14th) segment be considered as a part of the head, this breastbone might be taken for the mentum, in analogy to the horny mentum of the larvae of the *Tipulariae*."

Pseudopods. These are rounded, somewhat nipple-like processes, most prominent on the thoracic segments and usually in double pairs on the segments. Segment I has a pair on each anterior side of the spatula and bordered anteriorly by the imaginal leg discs; segments 2 and 3 have each a more prominent double pair, transversely arranged in the middle of the segments and likewise bordered anteriorly by the leg discs, those of the wings being lateral; segment 4 has an inconspicuous pair of pseudopods; segment 10 some indistinct protuberances; while on segment 11 are a pair of rather widely separated protuberances anterior to the anal slit. The last or 12th segment is terminated by two conical projections bearing a bristle at their apices.

Spiracles. There are nine pairs of spiracles, normally situated, one on the first thoracic segment and one each on segments 4–11. The last pair is placed apparently on the last segment, but Osten Sacken (14) has pointed out that this segment is in reality the 8th abdominal, the 9th being in *C. pini* and *C. pini-inopis*, (the latter being considered a synonym of *C. resinicola*) unusually

small and concealed under the 8th abdominal segment. The spiracles are horny, conical projections placed somewhat above the lateral line, especially on segment 1. The anal spiracles are far larger than the lateral ones, and are of most importance to the larva. They are truncated conical, with four stout spines. No young larvae were examined, but Eckel (5) says of the related *resinicola*: "The tracheal system undergoes no change with the larval growth except the odd development about the anal spiracles." In the young *resinicola* larva each terminal spiracle is a long horny tube, whereas in full-grown specimens they resemble those of *resinicoloides*. The 3rd thoracic segment has no spiracles although the tracheal tube is present here and well developed. Eckel has noted this in the eastern species.

Hairs and Bristles. These may be divided into two classes: (1) longer sparse hairs; (2) shorter numerous bristles. Those of the first class are, as far as could be ascertained, present on all but the supernumerary segment. On segments 4–10 are two larger hairs situated one below the other, the first close to the base of the spiracle. On segment 11, laterally and just below the spiracle is a large hair. On segment 12 are two apical hairs already referred to. These hairs, commonly near the spiracles, may assist in keeping the latter clear of the soft resin in which the larva lies.

The bristles* are arranged in transverse rows forming long patches on the dorsal and ventral surface of the body and thinning out laterally. Dorsally these bands are on the anterior portion of segments 2, 3, 4, 5 and 6, and on the posterior part of segments 8, 9, and 10. The band is heaviest on segment 4 where a blank space cuts out a broad mesal notch on its posterior border. On segments 2 and 3 the band is broad and almost divided by a transverse space, and on segment 5 is further reduced to three patches. The patch on segment 6 is almost obsolete. These bristles point posteriorly while the simple bands on segments 8, 9 and 10 have them pointing anteriorly.

Ventrally the bristle rows are not broken up but are simple, and are present on the anterior part of segments 2, 3, 4, 5, 6, 7, 8 and 9 where they point posteriorly and on the posterior portion of segments 4, 5, 6, 7, 8, 9, 10 and 11, where they point anteriorly. These rows pointing forward thin out anteriorly, and on seg-

* Illustrated in Ent. News, XX, Jan., 1909, Plate I.

ment 4 are quite small and inconspicuous, whereas the sets pointing backward become thicker anteriorly. We see then that these rows of bristles are heaviest at either end of the larva and absent or imperfectly developed along the middle of the body, there being a gradual transition from the posterior—to the forward—pointing bristles. The bristles thin out laterally and are more numerous on the venter than on the dorsum.

Although the larva is not an extensive traveller, it is nevertheless quite active and moves about considerably within the limited space of the resinous mass in which it lives. It cannot survive very long when completely submerged in the gummy exudation, but lives with its anal spiracles at the surface of the mass or in a hollow therein, while its mouthparts are in close proximity to the abraded cambium. It must also turn itself around in its cocoon before pupation. It was observed that the posterior portion of the larva is usually more extended and the cephalic end often more contracted. When the larva desires to advance, its anterior segments are extended, thus exposing the strong rows of backward-pointing bristles, while the hinder end is somewhat drawn in, thus concealing its bristles, and, by contracting and expanding the anterior segments the desired movement can be obtained. It would not seem of so much importance that the larva move its whole body backwards, but that it extend its caudal spiracles to an opening for air is quite imperative. Thus it could firmly anchor its cephalic end to a desired spot, and by means of the forward-pointing bristle rows extend its spiracles to the surface. By sufficient contraction the rows of bristles at one end could be completely concealed and those of the other end fully exposed and brought into play. The pseudopods may also assist in the movements of the larva.

INTERNAL ANATOMY.

Tracheal System. Pl. VI, Figs. 4 and 5. This was very carefully worked out, the tracheal arrangement being followed to the finest ramifications. As in other insects it consists of longitudinal trunks connected with the spiracles by lateral branches. Figs. 4 and 5 of plate VI shows this system from a dorsal and ventral aspect, of a larva submitted to some pressure under a coverglass. It consists of a pair of longitudinal dorsal trunks beginning at the spiracles of segment 1 and terminating in the caudal spiracles of segment 11. At G, Fig. 4, a stout branch is

sent ventrad, which divides almost immediately, the one branch proceeding to the head while the other, bending posteriorly, supplies the brain and sub-œsophageal ganglion. This posterior branch is F_1, in Plate VI, Fig. 4.

The two dorsal trunks are connected with the spiracles by short branches and are joined to each other in segments 4–9 and 11 by cross tubes, that of segment 11 being quite stout while the rest are slender and send out two re-dividing branches. These cross-tubes usually lose their striated appearance at their middle, appearing composed of two tubes fused together by a pair of sponge-like knobs. In segment 10, there is no fusion, the tubes remaining separate. Fig. 6, E_{10}, Pl. VI, shows a condition observed in two larvae in which the left branch is quite swollen basally, which perhaps was the normal thickness of both tubes, throughout before atrophy occurred and the tubes separated. The fact that in *C. resinicola* there are complete cross tubes in segments 4–11 would appear to strengthen this view. Furthermore it will be noticed that in *C. resinicoloides* the cross tube in segment 11 is quite stout and may substitute in a measure for the tubes in the above segment. Ramifying tracheae are apparently not so necessary in the last few segments.

The transverse lateral tubes D_3—D_{10}, Fig. 4, terminate in the spiracles except in segment 3 where there is no spiracle, in which case the tube disappears near the body surface. They are connected with one another either by the lateral longitudinal system through the short tube R_3, R_4, etc., as in segments 3–8, or they may run directly through the former, as in segments 9 and 10. This arrangement, however, is frequently asymmetrical.

The lateral longitudinal trunks arise from the dorsal ones in segment 2, Fig. 4, A_2, Pl. VI, and terminate as free branches in segment 10, C_{11}, Fig. 4, and apparently correspond to the ventral tubes as illustrated by Eckel (5), but differ widely from the latter in that they do not join the dorsal trunk posteriorly. They send out many branches F_2, F_3, K_4, K_5, etc., but the arrangement of these is not always constant. The primary function of the more anterior of these branches is to aerate and support the nervous system, that of the more posterior ones to supply the Malpighian tubules.

The ventral longitudinal system Fig. 5, Pl. VI, arises from the main dorsal one close to the anal spiracles in segment 11, and proceeding anteriorly commences ramifying in the middle of

segment 8, where it turns dorsally, closely following the Malpighian tubes to which short branches are sent.

Circulatory System. This system owing to its transparency and delicacy was quite difficult to follow, and so a detailed description of it cannot be presented. The dorsal vessel is a thin-walled, transparent tube which arises in front of and below the brain, and proceeds obliquely upwards until it meets the body wall in the posterior part of segment 4 where it is secured by the suspensorium. Thence it runs along the dorsum extending at least to the posterior transverse tracheal tube. It is divided into chambers and the valvular orifices (ostia) on either side open and close inwardly. The dorsal vessel pulsates especially in its anterior portion where there are several orifices. On each side of the heart in the middle of segment 4 is a strip of loose periçardial cells which proceed posteriorly, closely following the vessel.

Alimentary Canal. Pl. VII, Fig. 1. The alimentary canal consists of the long slender œsophagus D, the larger scarcely differentiated fore- and mid-stomachs (proventriculus and ventriculus) G, the slender and much curved ileum or small intestine I, the colon K, and the rectum L. A pair of long, recurved salivary glands C. F. open into the mouth, and two Malpighian tubules H, likewise recurved, are fastened to the fore part of the ileum. The whole system is supported chiefly by the tracheæ.

Lying above the œsophagus and salivary glands and extending well beyond the rods of the head skeleton is a large blind sac, S, Figs. 1 and 2, Pl. VI, which probably opens into the mouth. It contains in its middle a curious, dark purplish-brown object, A, Figs. 1 and 2, Pl. VI, which is lobed anteriorly, and posteriorly where it becomes semi-translucent and breaks up into small granules. This object is evidently the "*point oculiforme*" of Giard (8), who noted it also in a Cecidomyia, but what its function is he does not state. The large blind sac is apparently not muscular, though it is possible that it may serve as a food reservoir. The "*point oculiforme*" suggests a strainer of some sort, especially if the sac were muscular. The œsophagus extends to the end of segment 3 as a very slender and delicate tube, and is chitinized within the rods of the head skeleton, C, Fig. 2, Pl. VII, and Fig. 6, Pl. VII.

The large, straight, muscular stomach extends from the 4th to the 8th segment inclusive, and its cellular coat is made up of

more or less regular longitudinal rows of large protruding cells. The whole canal, including the salivary glands and the Malpighian tubules is clearly visible through the larval body wall.

In the posterior portion of segment 8 the slender ileum arises abruptly from the thick ventriculus as a curved and folded tube. Its cellular wall consists of several rows of large cells distinct in the anterior orange portion, less so in the whitish translucent middle part, and disappearing in the slenderer hinder end, which opens into the delicate grayish colon. The rectum is a rather colourless tube of considerable length terminating in the anus on segment 11.

The extreme hind part of the canal probably functions but little, except perhaps when the larva is near pupation. It was not seen to contain any waste matter, and if the larva was submitted to considerable pressure under a coverglass no excrement would be discharged.

Glandular and Excretory Appendages of the Alimentary Canal. The salivary glands are of large size and extend along each side of the ventriculus to the middle of segment 6 where they recurve dorsally and proceed to the anterior end of segment 5, being fastened to the ventriculus at that point. The larger posterior portion of the glands are glassy white and of moniliforme aspect, with several rows of large glandular cells containing large nuclei. At about the middle of segment 3 the glands become narrower, lose their glassy, large-celled appearance, and twisting spirally downwards, then upwards, dilate abruptly into granular ampullae of a pale yellowish-white color. These are three in number, two larger posterior ones and a single inconspicuous anterior swelling. From this latter point the glands taper gently, and at about the posterior border of the supernumerary segment give place to the tracheoid ducts. These are short slender tubes and join to form the common duct, B, Fig. 2, Pl. VI, a short distance within the chitinous rods of the head skeleton.

Whether the secretion of the salivary glands of the larva produces an irritation in the plant tissue thereby causing a flow of resin, or whether "the twistings of perhaps a dozen spiny-skinned larvae smooth out a round cavity" (in the resin), "the irritation causing a constant supply of fresh resin," to use Eckel's own words as regards *C. resinicola*, is a difficult thing to determine. Giard (9) thinks that the "zymase" secreted by the salivary

glands of the Cecidomyid larva determines the gall. No gall is formed in the case of the pitch-inhabiting midges, but the salivary secretion in this case might well stimulate and maintain the resinous exudation.

Attached interiorly to the second ampulla of the salivary glands and stretching in a curve across the brain which it overlies very closely is a curious, loose ill-defined structure of granular appearance, F, Fig. VII, Pl. 2, and containing brown patches, especially towards the bases. This I believe is Weismann's "cell chaplet," which he defines thus: "It consists of a string of large cells closely united which hangs like a garland, free in the body cavity. Its two ends are connected with the salivary glands," etc. What its function is remains to be ascertained.

The Malpighian tubules are of a deep orange color and arise from the anterior end of the ileum immediately where the latter is joined to the ventriculus by a delicate membrane. The arrangement of these two tubules with regard to the ileum and colon is not symmetrical since the left one follows rather closely those two divisions of the proctodæum, while the right tubule is quite free. Fig. 5, Pl. VII shows the left tubule in its relation to the proctodæum. Arising from the ileum each tube proceeds dorsally but not quite in symmetry as the right tube bends anteriorly and outwardly while the left first curves somewhat posteriorly, P, Fig. 1, Pl. VII and then follows the common course. Each tube is closely appressed to the ventriculus to which it is slightly fastened and proceeds anteriorly past the middle of segment 7. Here however the left one by reason of its posterior bend does not reach quite so far forward as its mate, but terminates slightly farther posteriorly and ends somewhat beyond the middle of the colon. Both tubes run along the ventral tracheal trunks in their terminal portions.

Giard says (10):—"In all the larvae of the Cecidomyidæ which I have studied, these tubes, two in number are united into an elegantly recurved handle, and open near the anus, the proctodæum being excessively short." In *C. resinicoloides* the tubes end freely, as we have seen, and the proctodæum, if extended would probably at least be as long as the rest of the alimentary canal.

It may be well said here that the alimentary canal (and its appendages) of *C. resinicoloides* much resembles that of *Diplosis buxi* illustrated by Berlese (2).

Organs of Reproduction? At about the termination of the Malpighian tubules, and below the same is a pair of elongate, fusiform, transparent bodies terminating anteriorly and posteriorly as slender tubes. These bodies were not observed in all the larvae examined. They are probably the developing reproductive organs.

Nervous System. Plate VIII, Figs. 1 and 2. The nervous system is more specialized than in many other dipterous larvae, in that there is considerable cephalization of the ganglionic chain. This chain is composed of ten distinct ganglia, exclusive of the sub-œsophageal one, and extends from the middle of segment 2 to the middle of segment 4. It is supported chiefly by the converging branches of the lateral longitudinal tracheae, while the brain is kept in place and aerated largely by the stouter pair of tracheal branches, F_1, which arise from the main dorsal system.

The brain or supra-œsophageal ganglion consists of two lobes of larger size than the rest and broadly joined to the sub-œsophageal ganglion, the commissure not being apparent. The œsophagus passes between these two ganglia, as probably also the dorsal vessel, the salivary glands running on either side. At least one pair of nerve cords from the brain, and two or more from the sub-œsophageal ganglion proceed anteriorly, and each of the ganglia of the chain sends out several nerves, some of which run along the lengths of the supporting tracheae. The last ganglion of the chain is more elongate than the others.

Very little could be made out of the sympathetic nervous system, and the paired ganglia, C, Figs. 1 and 2, Pl. VIII, arising posteriorly from the lobes of the brain are all that I feel sure of.

Musculature. The muscles were not studied though it was observed that they were numerous and well developed, a condition quite necessary in such a restless insect. Several muscles are fastened to the chitinous prongs of the head skeleton, and a number of large muscles radiate from the caudal cleft, being fastened to the body wall. Thus the larva is enabled to retract quickly its caudal end into the resinous mass if disturbed.

Adipose tissue. This is very well developed, so much so indeed that it obscures in a great measure the different visceral systems. The fat body is of a dirty yellowish-white color, and consists of a loose network of lobes with long meshes, and is continuous throughout the body, thickest below the middle, thence tapering to either extremity, extending anteriorly to the base of the

first pair of spiracles, and posteriorly to near the anus. It is circumscribed and largely supported by the tracheal system. Some time before pupation this fat tissue loses much of its compactness, becoming more or less watery in appearance and assumes a reddish color.

Imaginal Discs of Wings and Legs. Plate VIII, Figs. 6 and 7. These are easily seen in large full-fed larvae where they appear as more or less circular discs attached to the body wall.

The wing-buds, Pl. VIII, Fig. 7, A_2A_3, are larger than those of the legs, lie very slightly above the lateral line of the body, and are supplied with branches of the lateral and dorsal tracheae. Both wing- and balancer-discs arise from about the middle of their respective segments, ending posteriorly in a lobe and tapering anteriorly into the body wall.

The three pairs of leg discs, Fig. 6 A_1, A_2, A_3, are situated on either side of the ventral line and are more distinctly circular in outline than the wing discs and more strongly and completely cut by an inner ring. They are supplied by small branches of the lateral tracheae.

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EXPLANATION OF PLATES.

All figures greatly enlarged.

PLATE VI.

FIG. 1. Dorsal view of head skeleton; S. blind sac; A, point oculiforme; O, œsophagus; B, salivary duct; N, nerve.

FIG. 2. Lateral view of head skeleton; S, blind sac; A, point oculiforme; B, tracheoid duct; O, œsophagus; N. nerve.

FIG. 3. Sternal spatula; A. A, A, dorsal view; B, lateral view.

FIG. 4. Dorsal view of tracheal system of mature larva; A_1—A_{11}, dorsal longitudinal trunk; B_{12}, ventral longitudinal trunk; C_2—C_{10}, C_{11}, lateral longitudinal trunk; D_3—D_{10}, lateral transverse tubes to spiracles; E_4—E_{10}, E_{11}, cross tubes; F, F_1, F_2—F_4, branches to nervous system; K_4, K_5, branches to nervous system; G, branch from dorsal trunk; H, branch to head; R_3, R_4, R_5, connecting branch between C and D; M, head; S, supernumerary segment.

FIG. 5. Ventral view of tracheal system of mature larva, lettering same as in Fig. 4, B_8, dorsal turn of ventral longitudinal trunk.

FIG. 6. Aborted cross tubes of Seg. 10.

PLATE VII.

FIG. 1. . Dorsal view of alimentary canal of mature larva; A, head; B, blind sac; C, ampullae of salivary glands; D, œsophagus; E, Weisman's cell chaplet; F, large-celled portion of salivary glands; G, ventriculus; H. Malpighian tubule; I, ileum; J, ventral longitudinal trachea; K, colon; L, rectum; M, anus; P, posterior bend of left Malpighian tubule

FIG. 2. Head skeleton and portion of salivary glands; A, antenna; B, head skeleton; C, œsophagus; D, common duct of salivary glands showing tracheal character; E, ampulla of salivary glands; F, Weisman's cell chaplet.

FIG. 3. Sagittal section through larva; A, adipose tissue; B, muscle; C, alimentary canal; O, œsophagus; I, ileum; P, Malpighian tubule; M, M_1, salivary glands; H, heart; S, blind sac.

FIG. 4. Cross trachea in segment 11 showing central spongy mass.

FIG. 5. Lateral view of proctodeum; A, posterior end of ventriculus; B, ileum; C, colon; D, rectum; E, anus; F, Malpighian tubule; L, L_1, slender portion of ileum; O, point of origin of Malpighian tubules.

FIG. 6 Chitinized portion of anterior end of œsophagus.

FIG. 7. Dorsal view of anal spiracles, 12—last segment.

PLATE VIII.

FIG. 1. Dorsal view of nervous system; A, sub-œsophageal ganglion; B, brain; C, one of the paired ganglia of the sympathetic system; F, trachea feeding brain and sub-œsophageal ganglion.

FIG. 2. Lateral view of nervous system; lettering as in figure 1. T. trachea.

FIG. 3. Cross section through posterior portion of larva; A, adipose tissue; B, muscle; C, ventriculus; H, heart; M, Malphigian tubule; L, L_1, slender portion of ileum corresponding to L, L_1, of Fig. 5, Plate VII.

FIG. 4. Cross section through ventriculus showing epithelial cells.

FIG. 5. Cross section through anterior portion of larva; A, adipose tissue; B, muscle; C. ventriculus; M. salivary glands; H, heart; F, pericardial fat cells.

FIG. 6. Ventral view of anterior portion of larva (portions of segments 1, 2 and 3) showing imaginal leg discs, A_1, A_2, A_3; B, dorsal longitudinal trunk of tracheal system; C, lateral longitudinal trunk; D, tracheal branch feeding brain, this is F_1, Fig. 4, plate VI.

FIG. 7. Dorsal view of portion of segments 2 and 3, showing imaginal wing discs, A_2 and A_3; B, dorsal longitudinal trunk; C, lateral longitudinal trunk.